http://www.urbanfischer.de/journals/saeugetier



Aspects of mother-kid behavior in Alpine chamois, Rupicapra rupicapra rupicapra

By Kathreen E. Ruckstuhl and P. Ingold

Department of Biology, University of Sherbrooke, Sherbrooke, Quebec, Canada and Department of Zoology, University of Bern, Bern, Switzerland

Receipt of Ms. 02. 10. 1998 Acceptance of Ms. 14. 01. 1999

Abstract

We studied mother-kid associations for 9 mother-kid pairs of alpine chamois (Rupicapra rupicapra rupicapra) from May to October 1991. Mother-kid distance was studied from birth to weaning of the young. We further investigated the spatial relationship between the kid and the closest alien chamois within a group throughout the 6 months. The synchronization of activities between the mother and her kid was also analyzed. When mother and kid were in the same group, they were next neighbors in 90 % of all observations. Mother and kid were closest to each other when lying, while they were furthest apart when mothers were grazing and kids lying. Mothers and kids spent most of their daytime in the same group. The synchronization of activities between the mother and her kid increased with increasing age of the young. Mother and kid maintained close contact throughout weaning. The close association of mother and kid throughout the first 6 months of life of the young likely evolved as an anti-predator behavior and is first maintained through suckling and later through synchronization of activities between mother and kid.

Key words: Rupicapra, mother-kid bond, ontogeny, synchronization

Introduction

Suckling behavior and particularly mother-young interactions such as synchronization of activities and maintenance of proximity are central for the development and survival of young ungulates, especially in the first few week after birth (Epsmark 1971; Geist 1971; Shackleton and Haywood 1985). Although lactation is the most important care mothers give to their offspring in the first few months of their life, guidance, transmission of knowledge, and the learning of social behavior can further benefit the young (Lent 1974; Richard-Hansen and Campan 1992; Richard-Hansen 1993). Especially during eagle (Aquila chrysaetos) attacks proximity to the mother or to a defending female can be crucial for chamois kids (Krämer 1969; Locati 1990). The time the young spend in the vicinity of their mother also seems to depend on the frequency with which they suckle (Shackleton et al. 1984; Shackleton and Haywood 1985). As suckling frequency declines, the mother-kid bond may loosen as well. In Rocky Mountain bighorn sheep, Ovis canadensis, lambs spend less time with their mother and more time in the company of other lambs when they are weaned (Berger 1979), although post-weaning mother-daughter associations occasionally occur at high population densities (L'Heureux et al. 1995).

Chamois kids belong to the 'follower' type (Lent 1974) and kids follow their mothers within a few hours of birth (COUTURIER 1938). Despite its evolutionary importance and ef-

fects on social ontogeny and group structure, the development of mother-offspring bonds in ungulates has received little attention, apart from studies on suckling behavior (ROBINSON 1980; CLUTTON-BROCK et al. 1982, 1989; OFTEDAL 1985; FESTA-BIANCHET 1988; WHITE et al. 1989; RUCKSTUHL and INGOLD 1994; HASS 1995). Although mother-kid bonds seem to be the strongest associations in chamois, descriptions on the ontogeny and strength of these associations are rare (KRÄMER 1969; RICHARD-HANSEN and CAMPAN 1992; RICHARD-HANSEN 1993). We do not know how proximity between mother and kid is maintained through ontogeny and how close mother-kid associations are compared to associations between the kid and an alien chamois.

The aim of this study was to obtain quantitative information on the ontogeny of spatial relationships and the synchronization of activities in mother-kid pairs. We further investigated the spatial relationship between kids and their closest neighbor, to evaluate the strength of the mother-kid bond in comparison to non-mother-kid associations.

Material and methods

Study area and animals

Nine individually marked female chamois and their kids were observed between May and October 1991, on the Augstmatthorn, Switzerland (see detailed description of the study site in Krämer 1969). The study area is in a game sanctuary where hunting is prohibited. Focal females were all tagged with yellow-colored plastic stripes glued around the horns. Kids were unmarked, but individually recognizable through pelage characteristics, scars, and size differences. Mothers were identified during suckles, as chamois only suckle their own offspring (Krämer 1969). Female home ranges were between 1 400 and 2 137 m above sealevel (Ingold and Marbacher 1991).

Date of birth was estimated to be mid-way between the last observation of a female without a kid and the first observation with a kid. One kid was born between June 3 and 12. The 8 other kids were born between May, 8 and 22. All observations were made from a point where most of the slope used by the focal females was visible. Observations were made with binoculars (10×40) and spotting scopes (30×60) . Ages of females were estimated through counting of horn annuli at capture. The females ranged in age between 4 and 13 years (see Tab. 1).

Data collection

Each mother-kid pair was observed for 2 to 9 days, depending on presence and visibility. A total of 52 days (346 hours) focal scan sampling observations (Altmann 1974) were carried out. If several marked females were visible at the beginning of observation sessions, the female with the least observation hours or days was chosen as focal animal. Observations lasted between 2 and 14 hours (Tab. 1). Long observation hours (>8 hours) on the same mother-kid pair lasted usually from dawn to dusk, shorter observation periods (<8 hours) were distributed evenly throughout the day.

The activity (walking, standing, lying, or grazing) of the kid, the mother, and the kid's closest neighbor, as well as the distances between mother and kid and the kid and its closest neighbor were written down every 15 minutes. From these scan samples we calculated the percentage of time mother and kid were next neighbors, and the percentage of time an alien chamois and the kid were next neighbors. Focal observations shorter than 5 hours were discarded from the analysis, because short observation periods may not reflect average activity budgets or inter-individual distances of females and their kid (especially because sample sizes per female are relatively small).

Distances between individuals were estimated in animal lengths (referred to as chamois lengths). The next neighbor is defined as the adult chamois, which was closest to the kid at the moment of sampling. Animals were determined to be in the same group if they were closer than 50 chamois lengths from each other. Distances or proximity between mother and kid were estimated, when both were lying or grazing or, when the kid was lying and the mother was grazing. Distances between the kid and next neighbor were only estimated when both were grazing. Most chamois kids in our study area were weaned by November (Ruckstuhl and Ingold 1994). We therefore describe the ontogeny of the mother-kid relationship from birth throughout weaning.

Statistical analyses

Mean distances between mothers and kids were calculated separately for each mother-kid pair for the first 6 months of life of the kid. Differences in proximity between mother-kid and kid-next neighbor were tested with ANOVA (SOKAL and ROHLF 1995). Differences in proximity were then tested each month using Mann-Whitney U-tests (SIEGEL and CASTELLAN 1988) and Bonferroni adjusted significance levels. The effect of kid age (in months) and individual differences on the distances between mother-kid pairs were calculated using 2-way-ANOVA.

Some mother-kid pairs were sampled more than once per month. We therefore calculated the mean percent time mothers and kids had the same activity in a given month, to reduce pseudo-replication (Machlis et al. 1985; Leger and Didrichsons 1994). We calculated the percent time females and their kids had the same activity. Percentages were arcsine square-root transformed (Zar 1984). Medians are given with interquartile ranges, means are given with standard deviations.

Results

If mother and kid were in the same group, the kid was always closer to its mother than to any other adult throughout the first 6 months of life, except in September (F = 41.33, df = 1, p < 0.001; Fig. 1). Mother and kid were neighbors in 90 % of all observations throughout the summer (Fig. 2). When grazing, the kid always followed its mother. The distances between mother and kid were therefore small (Fig. 3 a). The apparent increase in distance between mother and kid from the 4th to the 6th month was due to individual differences (F = 3.06, df = 8, p < 0.001) in mother-kid pairs and was not age-related (F = 0.63, df = 1, p = 0.44).

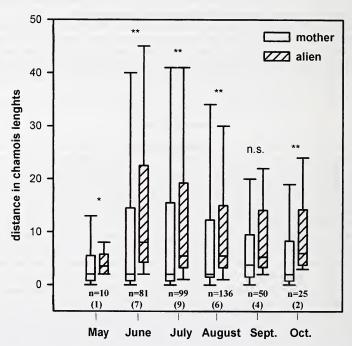


Fig. 1. Distances in chamois lengths between mother and kid, and between the kid and the next alien female from May to October 1991, Augstmatthorn, Switzerland. Number in brackets = number of mother-kid pairs, n = number of estimated distances. * = p < 0.05, ** = p < 0.001, n. s. = no significant difference (Mann-Whitney U-test, two-tailed). Box plots represent maxima, medians and minima with interquartile ranges.

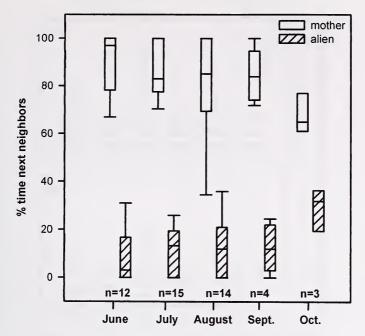


Fig. 2. Percent of observations when the next neighbor of a chamois kid was either its own mother or an alien female. n = observation days. Box plots represent maxima, medians and minima with interquartile ranges.

During the first 6 months of life of the kid mother and young most often lay in body contact with each other. The median distance therefore was often 0 chamois lengths (Fig. 3b). In general it was the kid who actively searched body contact with its mother. Except in two observations the mother was the first to bed down and the kid then lay down beside her.

Adult females grazed for longer and more frequently than their kids. After a longer lying phase, but also when the mother was grazing, the kid often remained bedded. Therefore the mother automatically increased the distance between her and her young while grazing (Fig. 3c). Hence greater distances were observed when the kid was lying and the mother grazing than when both had the same activity. As distances between mother and kid showed, they usually stayed in close proximity to each other when they were in the same group.

Mother and kid did not only spend most of their time in the same groups, but they also were closest to each other (Figs. 1 and 4). The percent time mother and kid spent in the same group during a day varied between and within mother-kid pairs (Tab. 1). While chamois number 4 was always seen in the same group as her kid during all observations (6 days), chamois number 6 was with her kid in less than 50 % of the observation period in 2 of 3 days. Longer periods of separation between mother and kid were rare but happened sometimes when mothers went to natural salt licks a few hundred meters from their preferred grazing grounds. Kids then stayed in the company of another mother and her kid. Separations between mother and kid could last up to 6 hours (2 observations). After a separation the mother always returned to the place where she had left her kid. If it was no longer there she started walking around in search of her kid often calling, and looking around. After the mother and kid reunited the kid attempted to suckle immediately.

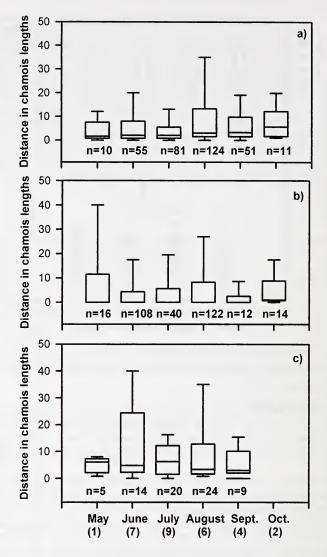


Fig. 3. Distances in lengths between chamois mother and kid when a) both were grazing or b) lying, and c) when the mother was grazing and the kid lying. n = number of estimated distances. Number in brackets = number of mother-kid pairs. Box plots represent maxima, medians and minima with interquartile ranges.

A kid's age affected the percentage of time mother and kid had the same activity ($F_{4,23} = 5.09$, p < 0.005). Mothers and kids were least synchronized in their activities in June (61 ± 16 % of observation time) and July (69 ± 8 %), more synchronized in August (78 ± 5 %) and September (78 ± 9 %) and most in October (86 ± 6 %; significant difference between June, July, and October: Scheffé post-hoc, p < 0.05). There were no individual differences in percent time spent in the same activity ($F_{5,22} = 0.85$, p = 0.53).

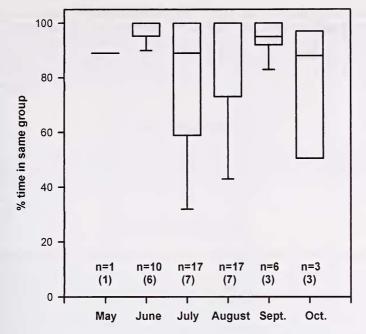


Fig. 4. Percent time chamois mothers and kids spent together in the same group during observations from May to October 1991, Augstmatthorn, Switzerland. n = observation days. Number in brackets = number of mother-kid pairs. Box plots represent maxima, medians and minima with interquartile ranges.

Discussion

Mother and kid maintained a very close proximity to each other in the first 6 months of the kid's life, as described for isard, *Rupicapra pyrenaica pyrenaica*, (RICHARD-HANSEN and CAMPAN 1992). They spent most of their time in the same group and were mostly next neighbors and therefore were closely associated. With increasing age the kid moved more freely within a group, probably in accordance with the increased time it spent grazing. The kid therefore sometimes was in the vicinity of an alien female, although it stayed most often close to its mother. The chamois is a follower type and the mother defends her kid against predators instead of relying on concealment as in the hiding types (Lent 1974). It is therefore important for the mother and her kid to stay in close proximity to each other (Krämer 1969). Suckling further increases the benefit to the young and maintains the strong bond between mother and offspring. Chamois often live in rugged terrain and the kid probably also depends on guidance through difficult terrain (Krämer 1969; Geist 1971).

Kids did not graze often in their first month of life and usually fed close to their mothers, decreasing the average mother-offspring distance. Interestingly, the distance between mother and kid on average was always shorter than the distance between the kid and an alien chamois, as suggested by Pachlatko and Nievergelt (1987). This is contrary to what we would expect if the process of weaning weakened the mother-offspring bond (Geist 1971). When mother and kid were separated the kid was never alone, but was with other kids in a 'kindergarten' or in the company of a 'baby-sitter' (Ruckstuhl and Ingold 1998). This might explain why kids on average are less than 10 animal lengths

Table 1. Percent time mother-kid pairs spent in the same group during observation hours, at the Augstmatthorn, Switzerland, 1991. Age = estimated age of the mother. % in same group = percent of the total observation time/day, when mother and kid were together in the same group.

Mother #	Age	Observation day	Observation hours	% in same group
1	5	July 7	5.5	91
1	5	August 4	5	100
2	5	August 3	10.5	52
2	5	September 19	5.25	100
2	5	October 3	5.25	100
3	13	June 26	9	97
3	13	August 12	6.25	100
3	13	August 20	8.5	100
3	13	September 16	10.25	95
4	8	July 1	5	100
4	8	July 2	7.25	100
4	8	July 28	9.25	100
4	8	July 30	7.25	100
4	8	August 15	9.5	100
4	8	August 22	5.5	100
5	8	July 11	5.25	100
5	8	July 20	6	83
5	8	August 7	9.5	37
5	8	August 13	11	73
5	8	August 27	13.5	93
5	8	September 20	6.5	69
6	11	August 14	7.75	84
6	11	August 21	7.5	43
6	11	October 10	10.25	39
7	5	June 11	8.25	88
7	5	July 20	8	69
7	5	August 5	6.75	100
7	5	August 22	8.25	100
8	8	July 30	5	85
8	8	August 16	9	96
8	8	October 4	8	100
9	7	June 22	8.5	97
9	7	July 23	7.5	100
9	7	July 30	8	69
9	7	August 13	7	64
9	7	August 16	6.25	96
9	7	October 11	9	89

away from the next alien chamois within their group. As suggested by RICHARD-HANSEN (1993) kids seem to be attracted by peers and often also approach adult females. Adult females often respond to such an approach by threatening with their horns or attacking (LOCATI 1990), leading to the greater observed distances between the kid and alien females compared to the kid with its own mother.

Synchronization of activity is crucial for group cohesion (Jarman 1974; Benham 1982; Rook and Penning 1991; Agesuma 1995). Mothers and kids were least synchronized in their activities (grazing/lying) in June and July and most synchronized in October. In the first few weeks kids do not spend much time grazing and mainly depend on their mothers' milk. As the kids grow older they increase the time spent grazing and therefore likely become more synchronized with their mothers. On the other hand kids suckle less often and for shorter periods in September and October (Ruckstuhl and Ingold 1994),

and the mother-kid bond could consequently decrease. Nevertheless, we observed a strong mother-kid bond in our study area throughout the season; which may have two different reasons: 1) in the first few months of life, the kid depends on the mother's milk and it therefore should have a strong incentive to stay close to its mother, 2) as the mother-young bond loosens up because of weaning, proximity may be maintained through increased synchronization of activities.

Acknowledgement

This study was financed through the Federal Game Department and the Game Department of the Canton of Berne. We are thankful to M. Festa-Bianchet and P. Neuhaus and an anonymous referee for comments on an earlier draft of this manuscript.

Zusammenfassung

Aspekte der Mutter-Kindbeziehung bei der Alpengemse (Rupicapra rupicapra)

Am Augstmatthorn im Berner Oberland, Schweiz, wurde vom Mai bis Oktober 1991 die Mutter-Kind Beziehung von Gemsen (*Rupicapra rupicapra rupicapra*) untersucht. Wenn Mutter und Kind in derselben Gruppe waren, so waren sie meistens nächste Nachbarn (außer im September) und verbrachten die meiste Zeit nahe beisammen. Die Aufrechterhaltung der Nähe schien von dem Kitz aus zu kommen. Die größten Distanzen zwischen Geiß und Kitz wurden gemessen, wenn die Geiß äste und das Kitz lag. Obwohl die Kitze mit zunehmendem Alter unabhängiger wurden, blieb die enge räumliche Beziehung bestehen. Mit zunehmendem Alter der Kitze waren Mutter und Kind in ihren Aktivitäten stärker synchron.

References

AGESUMA, N. (1995): Foraging synchrony in a group of Yakushima Macaques (*Macaca fuscata yakui*). Folia Primatol. **64**, 167–179.

ALTMANN, J. (1974): Observational study of behavior: sampling methods. Behaviour 49, 227-267.

Benham, P. F. J. (1982): Synchronization of behaviour in grazing cattle. Appl. Anim. Ethol. 8, 403–404.

Berger, J. (1979): Weaning conflict in desert and mountain bighorn sheep (Ovis canadensis): an ecological interpretation. Z. Tierpsych. 50, 188–200.

CLUTTON-BROCK, T. H.; Albon, S. D.; GUINNESS, F. E. (1989): Fitness costs of gestation and lactation in wild mammals. Nature 337, 260–262.

CLUTTON-BROCK, T. H.; IASON, G. R.; ALBON, S. D.; GUINESS, F. E. (1982): Effects of lactation on feeding behaviour and habitat use in wild Red deer hinds. J. Zool. (London) 198, 227–236.

Epsmark, Y. (1971): Mother-young relationship and ontogeny of behavior in reindeer (*Rangifer tarandus* L.). Z. Tierpsych. **29**, 42–81.

Festa-Bianchet, M. (1988): Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate, and sex. Anim. Behav. 36, 1445–1454.

GEIST, V. (1971): Mountain Sheep: A Study in Behaviour and Evolution. Chicago: Univ. Press.

Hass, C. C. (1995): Gestation periods and birth weights of desert bighorn sheep in relation to other caprinae. Southw. Naturalist 40, 139–147.

INGOLD, P.; MARBACHER, H. (1991): Dominance relationships and competition for resources among chamois *Rupicapra rupicapra* in female social groups. Z. Säugetierkunde **56**, 88–93.

JARMAN, P. J. (1974): The social organisation of antelope in relation to their ecology. Behaviour 48, 215–267.

Krämer, A. (1969): Soziale Organisation und Sozialverhalten einer Gemspopulation (*Rupicapra rupicapra*) der Alpen. Z. Tierpsych. **26**, 889–964.

Leger, D. W.; Didrichsons, I. A. (1994): An assessment of data pooling and some alternatives. Anim. Behav. 48, 823–832.

Lent, P. C. (1974): Mother-infant relationships in ungulates. In: Behaviour of Ungulates and its Relation to Management. Morges: IUCN 24, 14–55.

L'HEUREUX, N.; LUCHERINI, M.; FESTA-BIANCHET, M.; JORGENSON, J. T. (1995): Density-dependent mother-yearling association in bighorn sheep. Anim. Behav. 49, 901–910.

LOCATI, M. (1990): Female chamois defends kids from eagle attacks. Mammalia 54, 155-156.

Machlis, L.; Dodd, P. W. D.; Fentress, R.; Fentress, J. C. (1985): The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsych. 68, 201–214.

OFTEDAL, O. T. (1985): Pregnancy and lactation. In: Bioenergetics of Wild Herbivores. Ed. by R. J. Hudson and R. G. White. Boca Raton: CRC Press, Inc. Pp. 215–238.

Pachlatko, T.; Nievergelt, B. (1987): Time budgeting, range use pattern, and relationships within groups of individually marked chamois. In: The Biology and Management of Capricornis and Related Mountain Antelopes. Ed. by H. Soma. London: Croom Helm. Pp. 93–101.

RICHARD-HANSEN, C. (1993): Social interactions in Isard kids, *Rupicapra pyrenaica pyrenaica* (Artiodactyla: Bovidae): possible influence on development of social bonding. Ethology **94**, 291–305.

RICHARD-HANSEN, C.; CAMPAN, R. (1992): Social environment of Isard kids, *Rupicapra pyrenaica p.*, during their ontogeny. Z. Säugetierkunde **57**, 351–363.

ROBINSON, J. J. (1980): Energy requirements of ewes during late pregnancy and early lactation. Vet. Record 29, 282–284.

Rook, A. J.; Penning, P. D. (1991): Synchronisation of eating, ruminating, and idling activity by grazing sheep. Appl. Anim. Behav. Science **32**, 157–166.

Ruckstuhl, K.; Ingold, P. (1994): On the suckling behaviour of Alpine chamois *Rupicapra rupicapra rupicapra*. Z. Säugetierkunde **59**, 230–235.

Ruckstuhl, K. E.; Ingold, P. (1998): Baby-sitting in chamois: a form of cooperation in females? Mammalia 62, 125–128.

Shackleton, D. M.; Haywood, J. (1985): Early mother-young interactions in California bighorn sheep, Ovis canadensis californiana. Can. J. Zool. 63, 868–875.

Shackleton, D. M.; Peterson, R. G.; Haywood, J.; Bottrell, A. (1984): Gestation period in *Ovis canadensis*. J. Mammalogy **65**, 337–338.

Siegel, S.; Castellan, N. J. (1988): Nonparametric statistics for the behavioral sciences. 2. ed. New York: McGraw-Hill.

Sokal, R. R.; ROHLF, F. J. (1995): Biometry. 3. ed. New York: W. H. Freeman and Company.

White, R. G.; Holleman, D. F.; Tiplady, B. A. (1989): Seasonal body weight, body condition, and lactational trends in muskoxen. Can. J. Zool. 67, 1125–1133.

ZAR, J. H. (1984): Biostatistical Analysis. 2. ed. Englewood Cliffs: Prentice-Hall.

Authors' addresses: Dr. Kathreen E. Ruckstuhl, Dept. of Zoology (LARG), University of Cambridge, Downing Street, Cambridge CB2 3EJ United Kingdom and Prof. Dr. Paul Ingold, Ethology and Nature Conservation, Department of Zoology, University of Berne, Länggassstrasse 27, CH-3012 Berne, Switzerland.